Running head: Correlations of fatty acids among muscles

Genetic correlations of intramuscular fat content and fatty acid composition among muscles and with subcutaneous fat in Duroc pigs[1]

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ABSTRACT: There is an increasing interest in including intramuscular fat (IMF) content and fatty acid composition, particularly oleic acid content (C18:1), in the selection objectives of pig lines for quality pork markets. These traits are costly and can be measured in more than one location, so knowing their correlation structure across muscles and with subcutaneous fat (SF) is necessary for developing optimum sampling and recording schemes. We analyzed the genetic and phenotypic correlations of IMF content and composition among three of the most relevant muscles (LM; GM: *gluteus medius*; and SM: *semimembranosus*) and with the fatty acid composition of SF. All genetic correlations were positive but variable. For IMF, the genetic correlation between GM and LM was 0.68 and, for fatty acids, ranged from 0.62, for C18:1, to 0.82, for total polyunsaturated fatty acids. Genetic correlations of GM and LM with SM were much lower: 0.13-0.19, for IMF, and 0.10-0.54, for fatty acids. Correlations for fatty acid composition in SF with GM and LM were moderate to high (0.29-0.53 and 0.43-0.75, respectively), but null with SM. The expected responses for IMF in the three muscles and for C18:1 in each muscle and in SF to selection on records taken from only a single muscle or SF were estimated. Selection for IMF and C18:1 in GM is expected to lead to positive responses in IMF and C18:1 in LM and vice versa, although this can entail genetic lags of 20-45% in the muscle not directly selected for. Selection for C18:1 in SF is more effective for C18:1 in LM than in GM and of very limited value for IMF. In conclusion, the genetic correlations of IMF content and fatty acid composition among muscles and with SF, although positive, are variable enough to influence the genetic evaluation scheme for IMF and fat quality. They also indicate that GM and LM can be used alternatively for selection purposes.

Keywords: fatty acids, genetic parameters, intramuscular fat, oleic acid, subcutaneous fat, swine

INTRODUCTION

Intramuscular fat content (**IMF**) and fatty acid composition affect both the organoleptic and nutritional properties of pork and its derivatives (Wood et al., 2003). Particularly, oleic acid content (**C18:1**) has become an appreciated trait because of its association with flavour, technological properties, and health benefits (Toldrá, 2002; Christophersen and Haug, 2011; Jiménez-Colmenero et al., 2010). The strong economic importance of dry-cured ham in the Mediterranean area, where hams containing higher levels of C18:1 are premium-paid, together with the increased demand of healthy sources of meat, has triggered the interest of including IMF and fatty acid composition in the breeding goal of the pig lines producing for those markets. Because these traits are difficult and costly to measure, their genetic evaluation is usually based on indirect assessments (Jeremiah, 1998; Newcom et al., 2002, 2005) or on a limited number of records taken either on a single muscle (Ntawubizi et al., 2010; Ros-Freixedes et al., 2012) or from the subcutaneous fat (**SF**) (Fernández et al., 2003; Hofer et al., 2006; Gjerlaug-Enger et al., 2011). However, it is known that the pattern of fatty acid deposition may differ between IMF and SF (Duran-Montgé et al., 2008; Sellier et al., 2010; Bosch et al., 2012), across muscles (Sharma et al., 1987; Leseigneur-Meynier and Gandemer, 1991; Kim et al., 2008), and even among locations within a specific tissue (Faucitano et al., 2004). Thus, to develop adequate recording and genetic evaluation schemes for IMF and fatty acid composition traits, there is a need to know the correlation structure of these traits across valuable muscles and with SF. The objective of this study is to estimate the genetic correlation of IMF and fatty acids content across three economically relevant muscles (the loin and two muscles from the ham) and with

SF. The expected response for IMF and C18:1 in each muscle and SF to selection on records from only one of them is assessed.

MATERIALS AND METHODS

All experimental procedures were approved by the Ethics Committee for Animal Experimentation of the University of Lleida.

Animals and Sample Collection

Data from a purebred Duroc line (Selección Batallé, Spain) were used for the analyses (Solanes et al., 2009; Ros-Freixedes et al., 2012). The line was completely closed in 1991 and since then it has been selected for an index including BW, backfat thickness (**BT**), and IMF. The data set used for the estimation of genetic parameters consisted of 111,305 pedigree-connected pigs, from which 102,915 had at least one recorded trait (Table 1). Pigs with records were born from 1996 to 2011. At approximately 75 days of age, pigs were moved to the fattening units, where they were penned by sex (8 to 12 pigs/pen) until slaughter. All pigs were performance-tested at an average age of 180 days for BW and BT. Backfat thickness was ultrasonically measured at 5 cm off the midline at the position of the last rib (Piglog 105, Herlev, Denmark). During the test period, pigs had ad libitum access to commercial diets. Since 2002, 1,204 of the purebred barrows used for producing dry-cured ham were taken for recording IMF and C18:1. These barrows were raised in 15 batches until slaughter at around 210 days of age. From 160 days onwards, the barrows were fed a commercial pelleted finishing diet (Esporc, Riudarenes, Girona, Spain) with an average composition of 17.4% crude protein, 6.01% fiber, and 6.44% fat (C16:0, 20.4%; C18:0, 6.9%; C18:1,

33.9%; and C18:2, 30.1%). At the end of the finishing period, all barrows were slaughtered in the same commercial slaughterhouse at ~125 kg of BW. Immediately after slaughter, a sample of SF (n=333) and muscle semimembranosus (**SM**, n=198) was collected. After chilling for about 24 h at 2ºC, samples of muscles gluteus medius (**GM**, n=1,204) from the left side ham and LM at the level of the third and fourth ribs (n=318) were also collected. Samples of SF were collected at the same location than either the LM (n=203) or the GM (n=130) samples. Samples were immediately vacuum packaged, and stored at -20ºC until required for IMF and C18:1 determination. A summary of the population characteristics and number of records, sires, dams, and litters used for each analyzed trait is given in Table 1.

Fat Analysis

After muscle samples were completely defrosted and vacuum drip losses were eliminated, the dissected muscle, trimmed of subcutaneous and intermuscular fat, was minced. A representative aliquot from the pulverized freeze-dried muscle was used for fat analysis. Intramuscular fat content and composition was determined in duplicate by quantitative determination of the individual FA by gas chromatography (Bosch et al., 2009). Fatty acid methyl esters were directly obtained by transesterification using a solution of 20% boron trifluoride in methanol (Rule, 1997). Methyl esters were determined by gas chromatography using a capillary column SP2330 (30 m × 0.25 mm, Supelco, Bellefonte, PA) and a flame ionization detector with helium as carrier gas. Runs were made with a constant column-head pressure of 172 kPa. The oven temperature program increased from 150 to 225ºC at 7ºC per min and injector and detector temperatures were both 250ºC. The quantification was carried out through area normalization after adding into each sample 1,2,3-tripentadecanoylglycerol as internal

standard. Intramuscular fat content was calculated as the sum of each individual FA expressed as triglyceride equivalents (AOAC, 1997). Total saturated (**SFA**), monounsaturated (**MUFA**), and polyunsaturated (**PUFA**) fatty acids content, as well as individual C18:1, were expressed as their percentage relative to total FA in IMF. Fatty acids were identified by comparing their relative retention times with those of the external standard and confirmed by comparing their mass spectra to the computer library of the GC/MS database Wiley 275.L and NBS 75 K.L. Fatty acids were analyzed on a simple quadrupole instrument (GC/MSD 6890N-5973N, Agilent Technologies, Wilmington, DE) equipped with an electron ionization source using the same temperature program as described above. Scanned mass range of FA was m/z 35-450 and the scanning rate 3.46 scans/s. Fatty acid profiles of SF were analysed following the same procedure. Means and standard deviations by tissue are shown in Table 1.

Estimation of Genetic Parameters

Genetic parameters for IMF and C18:1 in GM, LM, SM, and SF were estimated fitting 4-trait multivariate models, where BW and BT were the two first traits and IMF or C18:1 in two different tissues the other two. In matrix notation, the model was:

$$\mathbf{y}_i = \mathbf{X}_i\mathbf{b}_i + \mathbf{Z}_i\mathbf{a}_i + \mathbf{W}_i\mathbf{c}_i + \mathbf{e}_i,$$

where $\mathbf{y}_i$ is the vector of observations for trait i; $\mathbf{b}_i$, $\mathbf{a}_i$, $\mathbf{c}_i$, and $\mathbf{e}_i$ are the vectors of systematic, additive genetic, litter, and residual effects, respectively; and $\mathbf{X}_i$, $\mathbf{Z}_i$, and $\mathbf{W}_i$ the known incidence matrices that relate $\mathbf{b}_i$, $\mathbf{a}_i$, and $\mathbf{c}_i$ with $\mathbf{y}_i$, respectively. Systematic effects for BW and BT were the batch (1,226 levels), gender (3 levels; males, females, and castrates), and age at measurement as a covariate. The model for IMF and C18:1 only included the batch (15 levels) and age at measurement. Because there were only 1.2 piglets/litter with records on IMF and C18:1 in LM, SM, and SF, litter was dropped

from the model for these two traits. Genetic correlations between IMF and C18:1 in different tissues were estimated fitting 6-trait (or 5-trait) multivariate models including, besides BW and BT, IMF and C18:1 in two different tissues (only IMF in one muscle if the other tissue was SF). The genetic parameters were estimated in a Bayesian framework using Gibbs sampling with the TM software (Legarra et al., 2011). Observed phenotypes and missing records imputed by data augmentation were assumed to be conditionally normally distributed as follows:

$$\begin{bmatrix} y_1 \\ y_2 \\ \dots \\ y_n \end{bmatrix} | \, \mathbf{b}_1,\mathbf{b}_2,\dots,\mathbf{b}_n,\mathbf{a}_1,\mathbf{a}_2,\dots,\mathbf{a}_n,\mathbf{c}_1,\mathbf{c}_2,\mathbf{R} \sim \mathrm{N}\left(X \begin{bmatrix} b_1 \\ b_2 \\ \dots \\ b_n \end{bmatrix} + Z \begin{bmatrix} a_1 \\ a_2 \\ \dots \\ a_n \end{bmatrix} + W \begin{bmatrix} c_1 \\ c_2 \end{bmatrix}, R \right),$$

where **R** was the (co)variance matrix. Sorting records by trait, and pig within trait, **R** could be written as $\mathbf{R_0} \otimes \mathbf{I}$, with $\mathbf{R_0}$ being the $n \times n$ residual (co)variance matrix between the n traits analyzed and **I** an identity matrix of appropriate order. Flat priors were used for $\mathbf{b}_i$ and residual (co)variance components. Additive genetic and litter values, conditionally on the associated (co)variance components, were both assumed multivariate normally distributed with mean zero and with (co)variance $\mathbf{G} \otimes \mathbf{A}$ and $\mathbf{C} \otimes \mathbf{I}$, respectively, where **A** was the numerator relationship matrix, **G** was the $n \times n$ genetic relationship matrix between the n traits, and **C** was the 2×2 (co)variance matrix between litter effects of BW and BT. The matrix **A** was calculated using all the pedigree information. Flat priors were used for additive and litter (co)variance components. Statistical inferences (means and highest posterior density intervals at 95% of probability (**HPD95**)) were derived from the samples of the marginal posterior distribution using a unique chain of 1,000,000 iterations, where the first 500,000 were discarded and one sample out of 100 iterations retained. Statistics of marginal posterior distributions and the convergence diagnostics were obtained using the BOA package

(Smith, 2005). Convergence was tested using the *Z*-criterion of Geweke (Geweke, 1992) and visual inspection of convergence plots.

Prediction of Expected Responses

The expected genetic responses for IMF and C18:1 were evaluated in a simulated breeding program based on records on either IMF or C18:1, or both simultaneously, taken from a particular tissue. For a given scenario, we assumed that only records from one of the tissues were available. Intramuscular fat and C18:1 were assumed to have the same economic weight when both traits were included in the selection objective. The simulated breeding program was a simplified version of that described in Ros-Freixedes et al. (2012). A population of 40 boars and 400 sows randomly mated was maintained on discrete generations. We assumed that 3 individuals per sire family were slaughtered to determine IMF or C18:1 or both. In each generation 25% of males and 50% of females were selected based on three half-sib plus pedigree records. Selection response was predicted deterministically by using the program SelAction (Rutten et al., 2002). The program accounts for reduction in variance due to selection (Bulmer, 1971) and corrects selection intensities for finite population size and for the correlation between index values of family members (Meuwissen, 1991).

RESULTS

The posterior mean of the genetic variance and the posterior mean and HPD95 of the heritability of IMF in GM, LM, and SM, as well as of the genetic correlations among them and with BT, are shown in Table 2. The corresponding posterior means

and HPD95 for fatty acid composition in GM, LM, SM, and SF are given in Table 3. The heritability of IMF in the three muscles was high, particularly for LM. Although they had wide HPD95 (due to the low number of pigs with data on these traits), all of them showed 95% probability of being greater than 0.30. The heritabilities of C18:1, SFA, MUFA, and PUFA in the three muscles were of similar magnitude than those for IMF. In GM and LM, the heritability estimates for SFA were the lowest and those for PUFA the highest. The heritabilities estimated in SF tended to be lower than those estimated in the muscles for all fatty acids. The genetic variance of fatty acids was much higher in SM than in GM, LM, and SF.

The genetic correlation between IMF in GM and LM was high (0.68), but it decreased to ~0.15 for that between them and SM. Unlike for GM and LM, the HPD95 for the genetic correlation between IMF in SM and IMF in GM and LM included null and negative values, thereby indicating very little evidence of correlation between them. Similarly, BT was positively correlated to IMF in GM and LM (~0.40), but uncorrelated to IMF in SM. The phenotypic correlations showed the same trends, but lower in magnitude than the genetic correlations. For all fatty acid traits, the highest genetic correlations were also found between GM and LM (0.62 to 0.82). The genetic correlations of GM and LM with SM were also positive but more moderate (0.29 to 0.44 and 0.10 to 0.54, respectively). However, the genetic correlations of LM with SF were consistently higher (0.43 to 0.75) than those of GM with SF (0.29 to 0.53). No evidence of genetic correlation between SM and SF was found.

The genetic parameters for C18:1 adjusted for IMF are shown in Table 4. Adjusted estimates did not relevantly differ from the unadjusted estimates reported in Table 2. Including IMF of the involved muscles as covariates only slightly decreased the correlations among muscles, although increased those between muscles and SF.

Including IMF as additional traits in the multivariate model did not have any systematic effect on the genetic parameters.

The posterior mean and HPD95 of the genetic correlations of C18:1 in GM, LM, SM, and SF with IMF in the three muscles are given in Table 5. The IMF content of GM and LM were moderately correlated with the C18:1 content in the same muscles (0.47-0.52), except for IMF in GM with C18:1 in LM (0.24). The genetic correlations between C18:1 and IMF were much lower when SM was involved (ranging from 0.14 to 0.37), although C18:1 and IMF in SM were highly correlated (0.69). The IMF content in any of the three muscles was uncorrelated with C18:1 in SF.

The expected responses for IMF and C18:1 in the three sampled muscles and SF to selection on records from different tissues are shown in Table 6. The correlated response in IMF (or C18:1) in GM to selection for the same trait in LM, and vice versa, was 0.6-0.7 times the direct response obtained in the sampled muscle. For GM and LM, selection for C18:1 (or IMF) led to a correlated response for IMF (or C18:1, respectively) of around half of the response for the proactively selected trait. The correlated responses in SM to selection based on records on GD or LM were always very low. There was only a small opportunity cost for IMF and C18:1 (less than 20%) with respect to single-trait selection when both traits are measured and included in a selection objective with equal economic weights. Relevant genetic changes in C18:1 in SF were found only to direct selection or to selection for C18:1 in LM. Selection for C18:1 in SF led to the same correlated response in C18:1 in LM than selection for C18:1 in GM, but the first had the disadvantage that it was not accompanied by a correlated change in IMF.

DISCUSSION

Three economically relevant muscles were considered in this study, two of them located in the ham (GM and SM) and one in the loin (LM). Sampling of central LM for chemical analysis is laborious and depreciates the loin as a primal cut. Instead, a big sample of GM can be easily obtained on the cutting line from the superior edge of the ham at no cost. Because of this, GM has been frequently used as the reference muscle in studies conducted under field conditions (Casellas et al., 2010; Ros-Freixedes et al., 2012, 2013). It is also feasible to sample SM from its exposed surface at no cost, but this sampling scheme has the limitation that only allows obtaining small off-line samples. Since SF samples are much easier to obtain than muscle samples, SF has been often used as the reference tissue where to determine the fatty acid profile, both for research and genetic evaluation purposes (Fernández et al., 2003; Hofer et al., 2006; Gjerlaug-Enger et al., 2011). Although alternative non-destructive methods can be used in substitution of chemical determinations, such as near infrared technology (González-Martín et al., 2002, 2005), the nature of the problem still persists and it is still needed to know the correlation structure between target and measured muscles for IMF content and fatty acid composition. The present study investigates the genetic implications of using alternative muscles or SF for phenotyping IMF and fatty acid composition in pigs.

The estimates of the heritability were slightly higher than those previously reported (Suzuki et al., 2006; Casellas et al., 2010; Sellier et al., 2010) for IMF, C18:1, MUFA, and PUFA, but similar for SFA. Among muscles, GM and LM showed high correlations between them for IMF and fatty acids content, but not with SM, which were much lower, particularly for IMF and SFA. An explanation for this result is that SM is subjected to greater sampling errors. To avoid depreciation of the ham, SM was

sampled by cutting a small slice from the exposed surface of the carcass at the slaughterhouse. In contrast, a much bigger sample of GM and LM was obtained from the ham and the loin retail cuts, respectively. As a result, samples from GM and LM are likely more representative of the whole muscle than the small slices of SM. This result would confirm that sampling can be a critical factor for an adequate interpretation of the correlations across muscles (Bosch et al., 2009).

The genetic correlations of fatty acids content between muscles GM and LM were higher than those between them and SF, in line with the results of Cánovas et al. (2009), who found different expression patterns between IMF and SF. The only exception was the correlation between SFA in LM and SF. In general, the correlations of fatty acid composition between LM and SF were higher than those between GM or SM and SF. This can be attributed to the fact that SF samples were mostly collected at the same anatomical location as LM, thereby suggesting that SF composition correlates better to the IMF composition of an adjacent muscle. In line with this, the remaining SF samples were taken at the same location as GM and, consequently, SF showed a higher correlation with GM than with SM. Note, however, that, due to the low number of samples at each location, genetic parameters for SF are based on pooled estimates at both locations. An additional source of sampling error may be incurred by sampling SF across fat layers. Although it is known that fatty acid composition differs between SF layers, its effect on the estimates of genetic parameters is likely small. For the main fatty acids, Suzuki et al. (2006) found that the correlation between the inner and outer SF layers was very high, from 0.84 to 0.96. The correlation structure of IMF fat content and composition with BT and SF composition has practical implications. On one hand, it indicates that there is room for improving IMF content independently from overall fatness (Tribout et al., 2004; Solanes et al., 2009; Ros-Freixedes et al., 2013), but, on

the other hand, that measuring fatty acids content in SF can be a good criterion for improving IMF traits only in certain retail cuts. Thus, regarding C18:1, SF (as measured in this study at the level of the third and fourth ribs) could be a good criterion for loin but not for ham.

The IMF content is known to affect fatty acid composition, being positively related to SFA and MUFA and negatively to PUFA (Wood et al., 2008; Ros-Freixedes and Estany, 2014). Using C18:1 as an example, genetic parameters were adjusted for IMF of the involved muscles, including them either as covariates in the respective models or as additional traits in a multivariate approach. In general, the estimates based on (co)variances adjusted for IMF as a covariate were lower than those obtained when adding IMF as additional traits. Although the interpretation of this result is not straightforward, what is important here is that the differences of both approaches with the unadjusted estimates are minor, particularly in terms of HPD95.

Results in the literature regarding the correlation of IMF and fatty acid composition among tissues are scarce but in line with those obtained here. Rauw et al. (2012) reported a phenotypic correlation of IMF between GM and LM higher than ours (0.69), but in contrast, for the correlation among the main fatty acids, their estimates were below our lower HPD95 limit, with values below 0.38. A genetic correlation of 0.65 between IMF in GM and LM and much lower ones with BT (0.36-0.38) were found by Hernández-Sánchez et al. (2013) using genomic markers information. These estimates were similar to ours. The phenotypic correlations reported by Yang et al. (2010) between LM and SF in a White Duroc × Erhualian cross were in the same range of values than ours (their values were included in our HPD95), with the exception of SFA, which were lower. Cameron and Enser (1991) reported much lower values for C18:1 (0.19) but more moderate for the main SFA and PUFA (0.31-0.54), using data

from Duroc and Landrace. These latter results are in contrast with those obtained by Suzuki et al. (2006) in Duroc for the genetic correlation of MUFA and SFA between LM and SF (~0.70). For PUFA, this genetic correlation was as low as ~0.18. Although part of the discrepancies among estimates may be explained by the age of the pigs, much younger in Cameron and Enser (1991) as compared to other works, and part by the relatively high standard errors associated to them, they provide sufficient evidence indicating that the pattern of fat deposition can differ widely across muscles and fat tissues.

Low correlations between muscles have also been found for other meat quality traits. Huff-Lonergan et al. (2002), in Large White, reported phenotypic correlations of 0.47 and 0.30 between LM and SM for pH and color (Hunter L) at 24 h post-mortem, respectively. Similarly, Gjerlaug-Enger et al. (2010) reported high genetic correlations (~0.8) between ultimate pH in GM and LM, both in Landrace and Duroc, but the estimates between these muscles and gluteus profundus were only in the range of 0.10 to 0.55. The phenotypic correlations among these three muscles did not exceed 0.5. As in our study, correlations were positive but moderate in magnitude.

It has been shown that there is room for improving IMF and fatty acid composition of pork through genetic selection (Ros-Freixedes et al., 2012). This involves setting up a feasible routine of recording these data on a commercial basis. The definition of an optimum design for such schemes requires knowing the correlation structure of IMF and fatty acid composition among target and sampled tissues. One of the main costs of sampling is the depreciation cost, which is likely to occur if measures are taken from the inner side of a high value retail cut such as loin. For its sampling simplicity, an alternative is to sample a portion of GM from the superior edge of the hams. Although it implies an opportunity cost with respect to LM, the target muscle, our

results indicate that selection based on GM still leads to acceptable genetic gains in LM, both for IMF and C18:1. In some cases, however, selecting for C18:1 in SF can be a good criterion to increase C18:1 in LM without increasing IMF, at least if SF is taken at the same location as LM. However, in general, C18:1 in SF is of very limited value for improving IMF or its fatty acid composition. A full description of the consequences of alternative selection and sampling schemes must take into account both the economic value of each muscle and its relative proportion in the carcass, as well as the genetic variation of IMF and fatty acid composition traits within each of them (Faucitano et al., 2004).

In conclusion, the genetic correlations of IMF and fatty acid composition across muscles and fat tissues, although positive, are variable enough to influence the genetic evaluation schemes for IMF and fat quality. The results obtained indicate that, in terms of genetic response, GM and LM can be used alternatively as the reference muscle for selection purposes. Moreover, they also reveal that using fatty acid composition of SF as selection criterion should cause more changes in LM than in GM, but not in IMF.

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Table 1. Description of the data set used in the analyses.

Item	No. of pigs	No. of sires	No. of dams	No. of litters	Mean	SD
Pedigree	111,305	830	22,634	40,658	-	-
Traits[1]						
BW at test, kg	102,325	747	20,722	39,594	104.8	12.3
BT at test, mm	98,397	748	20,582	38,724	15.6	3.5
Muscle gluteus medius						
IMF, %	1,200	169	678	681	4.8	1.9
C18:1, % FA	1,204	171	680	683	44.9	2.9
SFA, % FA	1,204	171	680	683	36.3	3.5
MUFA, % FA	1,204	171	680	683	49.4	3.1
PUFA, % FA	1,204	171	680	683	14.2	2.6
Muscle longissimus dorsi						
IMF, %	318	90	264	264	3.5	1.2
C18:1, % FA	318	90	264	264	45.8	2.7
SFA, % FA	318	90	264	264	38.0	3.4
MUFA, % FA	318	90	264	264	50.5	2.6
PUFA, % FA	318	90	264	264	11.6	2.5
Muscle semimembranosus						
IMF, %	146	59	138	138	2.7	1.7
C18:1, % FA	196	69	170	170	44.3	5.0
SFA, % FA	196	69	170	170	34.3	4.8
MUFA, % FA	196	69	170	170	48.3	5.3
PUFA, % FA	196	69	170	170	17.4	4.4
Subcutaneous fat						
C18:1, % FA	333	130	281	281	44.1	3.7
SFA, % FA	333	130	281	281	34.2	5.3
MUFA, % FA	333	130	281	281	47.3	4.0
PUFA, % FA	333	130	281	281	18.4	2.4
Covariates						
Age at test, d	102,915	748	20,848	39,837	179.3	10.6
Age at slaughter, d	4,317	392	2,480	2,633	207.2	16.1

[1] BT: backfat thickness; IMF: intramuscular fat; C18:1: oleic acid; SFA: saturated fatty acids; MUFA: monounsaturated fatty acids; PUFA: polyunsaturated fatty acids; FA: total fatty acids.

Table 2. Genetic variance, heritability (diagonal, in bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for intramuscular fat content (IMF) in three muscles and backfat thickness (BT).

Trait	Genetic variance	Genetic parameters[1]			
		IMF[2]			BT
		GM	LM	SM	
IMF, %					
GM	1.66	**0.51 (0.38, 0.65)**	0.68 (0.48, 0.87)	0.16 (-0.25, 0.56)	0.42 (0.24, 0.59)
LM	0.76	0.47 (0.38, 0.56)	**0.64 (0.44, 0.83)**	0.13 (-0.15, 0.42)	0.40 (0.14, 0.66)
SM	1.47	0.15 (-0.04, 0.33)	0.21 (0.02, 0.39)	**0.53 (0.30, 0.72)**	-0.09 (-0.53, 0.30)
BT, mm	4.35	0.29 (0.24, 0.34)	0.32 (0.23, 0.42)	0.04 (-0.12, 0.22)	**0.48 (0.46, 0.50)**

[1] Mean of the posterior density and, in parentheses, highest posterior density interval at 95% of probability.

[2] GM: gluteus medius; SM: semimembranosus.

Table 3. Genetic variance, heritability (diagonal, in bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for oleic (C18:1), saturated (SFA), monounsaturated (MUFA), and polyunsaturated (PUFA) fatty acid content in three muscles and subcutaneous fat (SF).

		Genetic parameters[1]			
		Muscle[2]			
Fatty acid	Genetic variance	GM	LM	SM	SF
C18:1, %					
FA[3]					
GM	1.92	**0.44 (0.32, 0.59)**	0.62 (0.41, 0.80)	0.40 (0.14, 0.65)	0.29 (-0.06, 0.72)
LM	2.13	0.54 (0.46, 0.62)	**0.59 (0.41, 0.80)**	0.30 (-0.08, 0.68)	0.52 (0.24, 0.78)
SM	12.69	0.24 (0.12, 0.37)	0.30 (0.13, 0.45)	**0.59 (0.39, 0.78)**	0.02 (-0.47, 0.60)
SF	1.83	0.34 (0.23, 0.45)	0.47 (0.31, 0.61)	0.09 (-0.16, 0.39)	**0.41 (0.22, 0.60)**
SFA, %					
FA					
GM	1.89	**0.42 (0.26, 0.57)**	0.73 (0.53, 0.91)	0.29 (-0.03, 0.58)	0.53 (0.21, 0.81)
LM	2.39	0.67 (0.60, 0.73)	**0.54 (0.36, 0.71)**	0.10 (-0.19, 0.46)	0.75 (0.57, 0.90)
SM	8.28	0.18 (0.04, 0.30)	0.15 (0.00, 0.28)	**0.57 (0.37, 0.78)**	0.00 (-0.52, 0.49)
SF	3.33	0.37 (0.27, 0.47)	0.63 (0.51, 0.74)	0.13 (-0.10, 0.38)	**0.46 (0.26, 0.65)**
MUFA, %					
FA					
GM	2.55	**0.50 (0.35,**	0.73 (0.56,	0.43 (0.18,	0.32 (-0.06,

		0.66)	0.88)	0.70)	0.66)
LM	2.56	0.62 (0.55,	**0.61 (0.45,**	0.30 (0.02,	0.58 (0.33,
		0.69)	**0.80)**	0.66)	0.79)
SM	14.63	0.28 (0.16,	0.30 (0.16,	**0.59 (0.41,**	0.02 (-0.42,
		0.41)	0.43)	**0.78)**	0.58)
SF	2.13	0.35 (0.24,	0.54 (0.40,	0.10 (-0.15,	**0.41 (0.22,**
		0.45)	0.66)	0.37)	**0.59)**
PUFA, %					
FA					
GM	2.79	**0.60 (0.47,**	0.82 (0.73,	0.44 (0.20,	0.41 (0.19,
		0.75)	0.92)	0.66)	0.63)
LM	3.23	0.76 (0.72,	**0.67 (0.48,**	0.54 (0.32,	0.43 (0.17,
		0.81)	**0.82)**	0.79)	0.68)
SM	10.30	0.38 (0.26,	0.47 (0.35,	**0.57 (0.37,**	0.11 (-0.28,
		0.49)	0.58)	**0.76)**	0.49)
SF	2.27	0.40 (0.31,	0.41 (0.25,	0.03 (-0.18,	**0.57 (0.37,**
		0.49)	0.55)	0.21)	**0.76)**

[1] Mean of the posterior density and, in parentheses, highest posterior density interval at 95% of probability.

[2] GM: gluteus medius; SM: semimembranosus.

[3] FA: total fatty acids.

Table 4. Heritability (diagonal, in bold), genetic correlations (above diagonal), and phenotypic correlations (below diagonal) for muscular oleic acid content (C18:1) adjusted for intramuscular fat content (IMF) and C18:1 in subcutaneous fat (SF). Adjustment for IMF was performed either adding IMF of the corresponding muscles as covariates in the model for C18:1 or as additional traits in a multivariate analysis[1].

	Muscle[2]			
Model	GM	LM	SM	SF
IMF as covariate				
GM	**0.41 (0.28, 0.55)**	0.56 (0.28, 0.82)	0.35 (0.10, 0.58)	0.31 (-0.07, 0.64)
LM	0.50 (0.42, 0.59)	**0.55 (0.34, 0.75)**	0.18 (-0.22, 0.60)	0.52 (0.25, 0.81)
SM	0.19 (0.06, 0.31)	0.19 (0.06, 0.33)	**0.59 (0.40, 0.79)**	0.14 (-0.22, 0.46)
SF	0.35 (0.23, 0.46)	0.47 (0.29, 0.62)	0.16 (-0.05, 0.36)	**0.44 (0.24, 0.63)**
IMF as trait				
GM	**0.47 (0.34, 0.60)**	0.64 (0.49, 0.80)	0.33 (0.11, 0.55)	0.32 (0.00, 0.62)
LM	0.55 (0.47, 0.62)	**0.61 (0.43, 0.80)**	0.36 (0.13, 0.59)	0.49 (0.15, 0.76)
SM	0.21 (0.10, 0.31)	0.30 (0.17, 0.43)	**0.62 (0.41, 0.82)**	0.18 (-0.24, 0.57)
SF	0.34 (0.23, 0.45)	0.47 (0.30, 0.62)	0.15 (-0.09, 0.38)	**0.45 (0.24, 0.65)**

[1] Mean of the posterior density and, in parentheses, highest posterior density interval at 95% of probability.

[2] GM: gluteus medius; SM: semimembranosus.

Table 5. Genetic correlations of intramuscular fat (IMF) and oleic acid (C18:1) content in different muscles and subcutaneous fat (SF)[1].

	C18:1[2]			
IMF[2]	GM	LM	SM	SF
GM	0.47 (0.27, 0.66)	0.24 (-0.04, 0.50)	0.29 (-0.02, 0.59)	-0.03 (-0.39, 0.32)
LM	0.51 (0.30, 0.71)	0.52 (0.31, 0.72)	0.37 (0.19, 0.55)	0.10 (-0.29, 0.41)
SM	0.15 (-0.15, 0.44)	0.14 (-0.14, 0.46)	0.69 (0.49, 0.86)	0.06 (-0.29, 0.42)

[1] Mean of the posterior density and, in parentheses, highest posterior density interval at 95% of probability.

[2] GM: gluteus medius; SM: semimembranosus.

Table 6. Direct (bold) and correlated (regular typesetting) expected genetic response for intramuscular fat (IMF) and oleic acid (C18:1) content in a given tissue to selection on records taken on different muscles or subcutaneous fat (SF)[1].

	Tissue and trait used as a selection criterion[2]						
	GM			LM			SF
Response[3]	IMF	C18:1	IMF+C18:1[4]	IMF	C18:1	IMF+C18:1[4]	C18:1
IMF[2]							
GM	**28**	12	**24**	20	7	15	-1
LM	18	14	20	**30**	15	**25**	2
SM	4	4	5	4	4	5	2
C18:1[2]							
GM	13	**26**	**23**	15	18	19	7
LM	7	16	14	16	**29**	**27**	13
SM	8	11	11	11	9	11	1
SF	-1	7	4	3	15	12	**25**

[1] In each generation 25% of males and 50% of females were selected based on three half-sib plus pedigree records.

[2] GM: gluteus medius; SM: semimembranosus.

[3] Genetic standard deviation units (×100).

[4] Same economic weights for both traits in the selection objective.